SOME MODIFICATIONS OF STEMS AND ROOTS FOR PURPOSES OF RESPIRATION.

HERMANN VON SCHRENK.

The conditions surrounding many of our swamp and marsh plants are such as to render the free absorption of oxygen a comparatively difficult matter. This applies particularly to the organs growing in the mud and water, the roots, rhizomes and bases of stems. In the majority of land plants oxygen is taken up by these organs through the epidermis by diffusion, and is carried from there to the cortical parts where it is needed. In the water this free diffusion is rendered difficult and often nearly impossible. In such cases we find the plant adapting itself by varying and changing its structure, so as to enable it to grapple with the new conditions.

Such variation may be in one of several directions (5), by increasing the absorbing surface, by facilitating diffusion by means of large intercellular spaces, or by producing organs or tissues better fitted to absorb the necessary gases. In the extended root system of Mikania and some of the palms we find an example of the first change, the stem of the water lilies may represent the second, and the tissues of *Decodon Verticillatus* (*Nesæa Verticillata*) *Jussiæa* complete the series.

Whether these plants, *i. e.* species, which are so modified, have shown such structure from the beginning of their existence is a question. We may recall the explanation of Shaler (1) with regard to the cypress knees. He considered the cypress a tree of earlier geologic times than our own, crowded into the swamps at the present time by more favored rivals. Here, under the adverse conditions of respiration, it developed the knees. On the hillsides, where the old conditions prevailed, no knees were formed. In the case of *Decodon*, *Lycopus* and others, I believe, we see something akin to this.

There are at present, then, a number of plants which have, in their later stages, contrivances or organs enabling them to obtain oxygen more easily than without such contrivances. The latter have become, in the majority of cases, recognized characters of their species, such as *Decodon*, *Jussiæa*, etc. The remaining ones seem to have a greater plasticity of organization in this respect. During the past year I had occasion to observe the habits of several of this class. *Lycopus sinuatus*, *Ell.* is a labiate growing in a variety of habitats, from dry borders of woods to deeper swamps. If a specimen from a dry location be taken, one will find the lower portion of the stem and the rhizome of about the same size as the aërial stem. The characteristic sclerenchyma fibres in the corners of the stem lie immediately below the epidermis. Specimens from a swamp show a very different structure. The lower portion of the stem is very much swollen apparently, decreasing in size as one leaves the water going upwards. Examination will show the epidermis ruptured in many places, often entirely gone, exposing to the surrounding air a mass of white, spongy tissue extending to the vascular ring. The tissue consists of elongated cells linked by smaller cells, forming a coarse network, as it appears, with large intercellular spaces, cavities one might almost call them. The origin of this tissue is similar to that found in *Decodon* (3). That the formation of this tissue is due directly to the position of the plant in the water, I am thoroughly convinced. Many specimens were collected near Southold, Long Island, growing at the edge of a pool in sphagnous ground. These had the "ærenchyma" tissue developed to a large extent. On a tree stump in this sphagnous ground other specimens of *Lycopus* flourished a foot or more above the water level. These had *no* sign of the tissue. In all there were some 20 individuals on this stump. Other stumps near by and in neighboring swamps gave the same result. A fact which I have observed, but am at present unable to explain, is that *all* individuals of this species growing in damp places do not develop the ærenchyma, as all individuals of *Decodon* do, for instance. One will often find in the same swamp some with, others without,

this tissue. I believe in some parts of the country the *Lycopus* never develops this tissue; in Central New York I was unable to find it.

The same may be asked of another plant, *Ludwigia Sphærocarpa*. This plant grows luxuriantly in the muddy borders of some ponds on Long Island. I collected it at Manor, L. I. The stems grow out from the mud with a layer of ærenchyma nearly one-half inch in thickness around them, the layer extending nearly a foot above the surface of the water. Its appearance is in every respect similar to the layer in *Decodon*, so similar that I mistook the plant for *Decodon* several times. I have not collected this plant sufficiently to say that it may grow without ærenchyma, as does *Lycopus sinuatus*, but it evidently does, to judge from such notes as "Bark below *often* spongy-thickened" * (italics my own) and others of similar nature. Some individuals on the bank in moist sand had less of the tissue than those in deep water.

Before proceeding to another group of plants I would record an instance of *Decodon Verticillatus* growing in a dried-up pond. I had no means of telling absolutely how long the pond had been dry, but it appeared to have been partially filled early in spring. The clumps of *Decodon* grew a foot above the pond bottom on tufts of Careces, many of the stems having bent over in the characteristic manner. The bases of the stems showed a very slight development of ærenchyma tissue, but every plant had some of it. The tissue was shrunken and to all appearances was dead, and had been so for some time. This is what one might have expected, the water gone, the need for aërating tissue was no longer there, and it ceased to function. It will be of interest to follow these plants in their next year's growth.

Besides the plants noticed so far, we find modifications for respiration in many shrubby plants, which may, as respects the adaptation, be classed with those in *Lycopus*, etc. The most striking example of this which I have been able to find, is the common elder, *Sambucus Canadensis*, L. This is in the true

* Gray's Manual, p. 188.

sense of the word not a swamp plant in most places. Its habitat is given by Gray as "rich soil in open places." It grows along fences and along stream banks. In Long Island its favorite habitat is on the borders of inlets from the bays and marshy banks of streams and ponds, oftentimes in water a foot deep. Fig. 1 represents a small plant taken from a pond near Eastport. One is struck by the great swelling which the stem has evidently undergone below the water. (*A-B* is the water line, the stem having grown somewhat obliquely.) All over the surface are snow-white excrescences of a warty nature, varying in size and shape. These decrease in size and number as one goes upwards from the water, and some inches above it one finds them merging over into the ordinary lenticels (Fig. 1, *L*.). The white spongy tissue is at once proven to consist of cork cells (Füllzellen) protruding from a structure of lenticellular character. These cells are developed from a meristem at a surprising rate; in many cases the protuberances were two inches in length, three-eighths inch wide, extending three-eighths inch above the surface. Fig. 3 represents a cross section of a small one of these water lenticels (2). It will at once become evident that we have here a modified lenticel. A meristem (*m*) forms beneath the epidermis, before the appearance of the phellogen layer, which gives rise to the ordinary "Füllzellen" (*F*). These are formed in rapid succession until the epidermis bursts. The activity of the meristem continues, pushing out large masses of these cells, which finally appear as a column between the two lips of the lenticel, the ruptured ends of the epidermis. Meanwhile the phellogen layer (*phel*) has formed and has given rise to the periderm (*perd*). Our figure shows a series of periderm cells formed, which are being crowded back by the rapidly increasing number of cork cells. The latter are filled with air, giving the whole mass its white appearance.

The growth of these structures continues, several unite, and then more, and we have at last long patches of this tissue of loosely connected cells extending all over the stem, leaving but little of the original bark (see Fig. 1) in position; it would take but little to form a continuous layer around such a stem, produc-

ing not peridermal cells, which resist the entrance of air, but a tissue exceptionally well fitted for the absorption of oxygen.

The water lenticels are by no means confined to the stem, but are very often found on roots. Lenticels occur but rarely on roots, and then only sparingly. But here we find them produced abundantly. The submerged stems develop large numbers of long fibrous roots, which branch sparingly. The roots grow out horizontally, rarely into the mud below. On them the lenticels are found. They differ in no respect from those found on the stems, except perhaps in size. A noteworthy fact is that in many cases the adventitious roots produced by the stems break through these lenticels (Fig. 1, *c*), and sections show these roots growing directly toward a lenticel from their very differentiation. This directive influence of the lenticel on such roots has often been noted, but is especially striking here where the lenticel has assumed such large size.

In addition to the water lenticels the *Sambucus* stem presents a modified cortex. The latter for some distance from the water consists of round cells filled with active protoplasm and numerous chlorophyll grains. The phellogen produces phelloderm cells (*phd.*) and thus increases the thickness of the cortex. Intercellular spaces are few and comparatively small, even under a lenticel. As one goes down the stem towards the water, these spaces become larger. The cells of the cortex, still green and full of protoplasm, become separated, and in the lower portions they form a loose, spongy tissue, very different from the cortex further up the stem. Here, too, the cells are more numerous, and this, together with the air spaces, makes the cortex seem twice as thick. This gives the whole stem the appearance of being of so much greater diameter in the water.

Fig. 3 represents a section taken near *D*, Fig. 1. Here the air spaces are quite marked (*sp*). They appear to originate near the phellogen layer, the new phelloderm cells parting from one another soon after their separation from the mother cell. It will be seen that this system of canals filled with air, thus closely surrounded by active protoplasmic cells, must insure to the fullest

extent the free diffusion of oxygen. Those passages are in close connection with the outside through the water lenticels, which offer little resistance to the available oxygen (Fig. 3). The exact manner in which the lenticels act to absorb the oxygen of the water is a problem yet to be solved. We have thus an arrangement whereby the stem is enabled to obtain oxygen in a manner both striking and efficient.

It may be asked, is it proven that these structures function as respiratory organs? The fact does seem certain, as the large quantities of air in the spaces and their connection with the outside seem to indicate. Another proof is seen in the fact, that they are *entirely* absent in plants not growing in the water. In individuals of *Sambucus Canadensis* taken from dry soil, I was unable to find any indications of the large intercellular spaces or the large development of lenticels.

Other shrubs and trees show similar changes. *Cephalanthus Occidentalis* is perhaps next in order. Its cortex shows spaces similar to those of *Sambucus* (Fig. 4). In these we find individual bast cells (*b*) torn away from the adjoining cells, some hanging loosely in the air space. The water lenticels are present in great numbers (Fig. 2), but differ in some respects from *Sambucus*. They are long, very narrow and occur in patches along the stem. The masses of " Füllzellen " extend further from the stem than those of *Sambucus*, sometimes as far as one inch from the bark. The roots of this plant were well supplied with lenticels.

Some of the larger trees showed the water lenticels in large numbers. On the roots of *Populus monilifera* they protruded from among the many fibrous roots. These lenticels showed the lateral portions of the structure well formed. On the roots of *Acer rubrum*, on which I first noticed these organs, they are very numerous, some 20 or 30 to the square inch. These are perennial. At the end of one year the cork column is perhaps one-eighth inch high. A layer is then formed, similar to that in the ordinary lenticel, closing the opening. This is pushed out in spring, with the cork of the preceding year, and a new piece is added to the column. This process may continue for many

years, so that an old root presents a peculiar appearance, especially in quiet water where the cork columns are not broken by the flow of water against them.

How many other plants may show these modifications one cannot tell, but I am confident that many more than we are at present aware of, will, upon close examination, prove to possess to a greater or less extent adaptation furthering respiration. The cases noted, especially *Sambucus* and *Lycopus*, show a plasticity of organization which seems striking. It would seem that to effect a change so marked upon a species, it would necessitate the continued action of the environment upon individuals. But here we have instances of plants responding to this action in the short space of two months or less. Exactly how soon this influence would make itself felt experimental evidence must bring forth. Individuals should be grown under different conditions of moisture, and hence of exclusion of oxygen, and the result ought to explain some of the questions concerning which we are still in doubt. The function of respiration has often been underestimated, and it seems that modifications of this kind would tend to emphasize the necessity of this function for the performance of the life activities. When plants of such different organizations produce changes of this kind, so marked and so constant, the importance of the end striven for must be recognized.

BIBLIOGRAPHY.

1. Shaler, N. S.—Notes on Taxodium distichum. Science, 1883.

2. Schenck, H.—Über das Aerenchyma, ein dem Kork homologes Gewebe bei Sumpfpflanzen. Pringsh. Jahrb. f. Wiss. Bot., Bd. XX., 1889, p. 526.

3. Schrenk, J.—On the floating tissue of *Nesœa Verticillata.* Bull. Torr. Bot. Club, Vol. XVI., 1889, p. 315.

4. Wilson, W. P.—The production of aërating organs on the roots of swamp and other plants. Proc. Am. Acad. Nat. Science, Philadelphia, 1889.

5. Rowlee, W. W.—The Aëration of Organs and Tissues in Mikania and other Phanerogams. Proc. Am. Micros. Soc., XV., p. 143.

(NOTE.—In this paper will be found a full list of papers relating to this subject.)

EXPLANATION OF PLATES.

PLATE I.

Fig. I. *Sambucus Canadensis*, L., base of stem with water lenticels; *A-B*, water level; *L*, lenticels, *C*, root growing from a lenticel. ×

PLATE I.

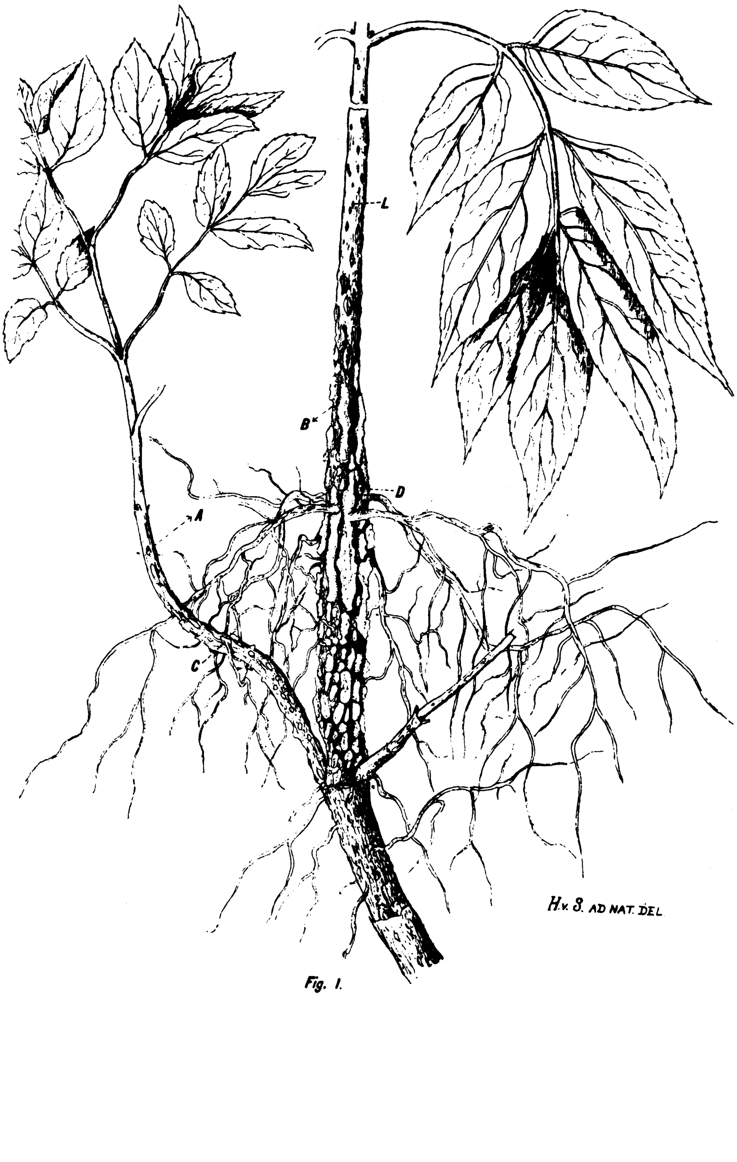

Fig. 1.

PLATE II.

Fig. II. *Cephalanthus Occidentalis,* L., base of stem showing upturned bark (*B*); at *A* some of the cork columns are seen projecting out from the stem; *C*, root with water lenticels. ×

PLATE II.

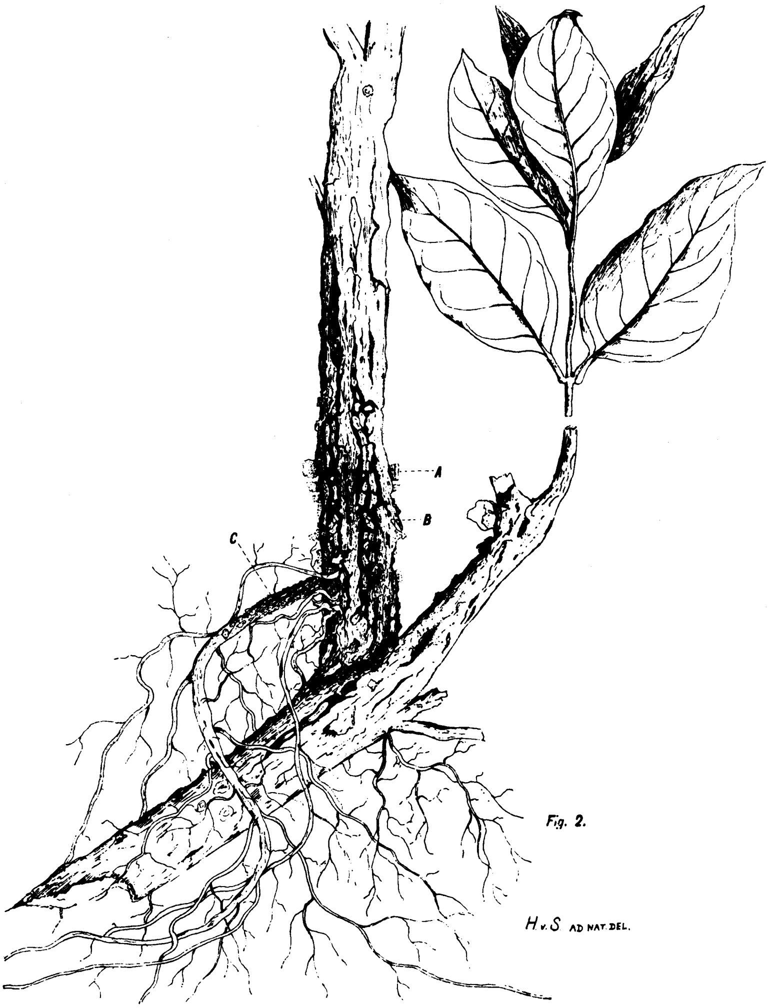

PLATE III.

Fig. III. *Sambucus Canadensis*, L.—transverse section through a water lenticel (about *D*, Fig. 1). *F*, "Füllzellen;" *m*, lenticel meristem; *perd*, periderm; *phel*, phellogen; *phd*, phelloderm; *sp*, air spaces; *b*, bast cells; *c*, cambium; *w*, wood.

Fig. IV. *Cephalanthus Occidentalis.*—Section taken immediately inside a water lenticel showing the air spaces, *sp*, with isolated bast cells, *b*.

PLATE III.

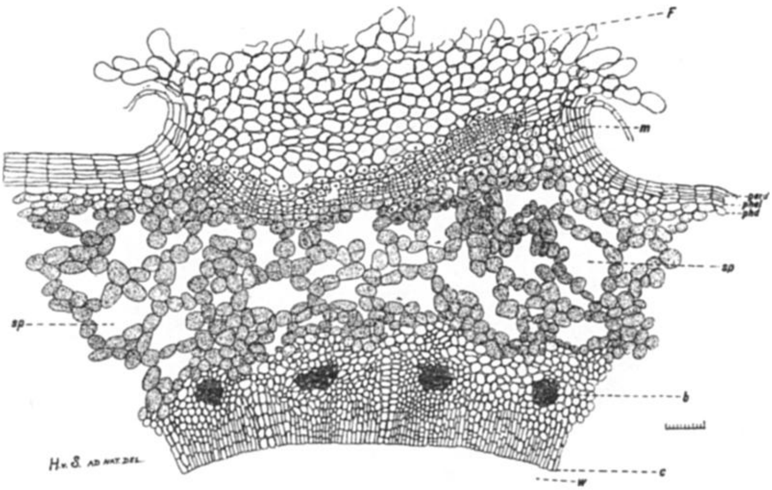

Fig. 3.

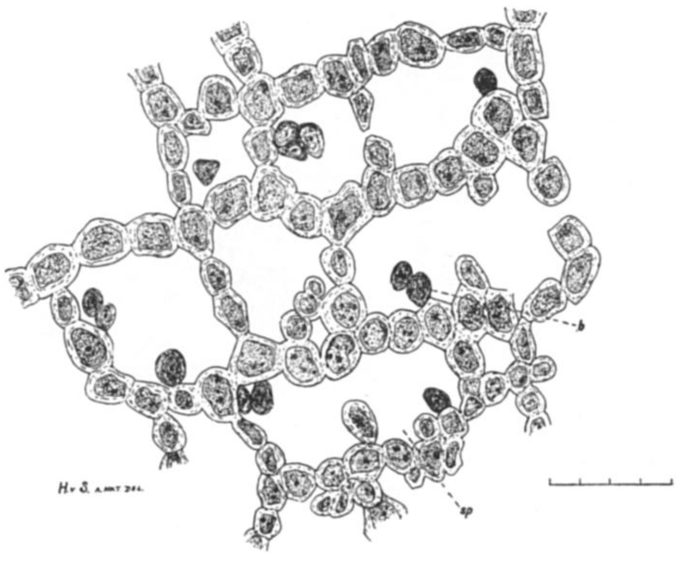

Fig. 4.